

Chapter 6

Evolutionary Genetics of Personality in Nonhuman Primates

Mark James Adams

6.1 Introduction

Our whole conception and acknowledgement of personality – both scientific and quotidian – is based on the notion of difference. A personality is precisely that which distinguishes one individual from another. These differences have consequences for behavior, health, and well-being, but we are mostly ignorant of their evolutionary roots. For humans and other primates, evidence is coalescing around a common structure that describes personality differences usefully categorizable in terms of shared versus derived traits and consistent with known species differences (Gosling and John 1999; Weiss et al. 2006). Although functional and genomic studies begin to hint at the proximate genetic and environmental factors that mix to produce differences in personality, we are still left with this wondrous puzzle: Why do these basic differences persist over evolutionary time scales as primates have speciated and evolved?

This problem runs up against one of the unendingly contentious issues in quantitative genetics: How is trait variation maintained? This question comes out of a basic mathematical result in genetics with its origin in animal breeding. The result says that natural and artificial selection reduces the heritability of a trait in a population. Much ink has been spilled on theoretical treatments of variation in primate (mostly human) personality and other psychological traits (e.g., Tooby and Cosmides 1990a; Nettle 2006; Penke et al. 2007). What we need are good data.

But which way forward? Which data? In evolutionary psychology, the usual tact is to identify past conditions within a lineage that explain present-day adaptation and variation (Tooby and Cosmides 1990b). This is mistaken in that it ignores a key insight of evolutionary biology: it is only through a phylogenetically informed approach that we can determine when traits arose and changed within a lineage (Gosling and Graybeal 2007). For determining when different features of personality originated in each primate lineage, this comparative approach is sound. To explain why differences

M.J. Adams (✉)

Psychology, School of Philosophy, Psychology and Language Sciences, The University of Edinburgh, 7 George Square, Edinburgh EH8 9JZ, UK
e-mail: m.j.adams-2@sms.ed.ac.uk

within populations persist, however, something else is needed. Evolutionary quantitative genetics fills this gap. This branch of biology deals with the effects of evolutionary processes on continuous traits and the genetic and environmental factors underlying them. Most promising and relevant for the explorations of primate personality is the development of techniques for studying evolution in wild populations using pedigree data (Kruuk and Hill 2008). Given the length of time many primate populations have been investigated (Goodall 1986; Rawlins and Kessler 1986; Fedigan and Asquith 1991; Nishida et al. 2002), the identification of individuals (de Waal 2003), and the resolution of pedigree structure (particularly through matrilineal kin e.g., Fairbanks et al. 2004; Blomquist 2009b), it is a wonder that these techniques have not been more widely applied to nonhuman primate behavior.

Revealing the evolution of nonhuman primate personality requires first understanding how personality variation is defined and how differences among species are informed by phylogenetic relations. The evolvability of personality within a species is proportional to the heritability of each personality trait, which has already been estimated in several primate species. Making usable inferences about the evolution of personality first requires choosing a method for estimating heritability appropriate to the data (Kruuk and Hadfield 2007). Knowing what heritability really is will lead to a consideration of the exact role that the resemblance between parents and offspring, as captured by heritability, plays in random drift and selection in wild populations. Pinning down the fitness implications of personality differences requires more than just the genetic structure of personality but offers the opportunity to integrate many threads from psychological and behavioral–ecological approaches to personality.

6.2 Nonhuman Primate Personalities

Nonhuman primate personality has been examined from a number of stances, but integrating these different attitudes is still a major challenge (Clarke and Boinski 1995; Itoh 2002; Uher 2008) (see Chap. 5 for a full discussion). These methods include, broadly, impressionistic ratings using adjectives describing personality; observational measures and codings of differences in the presence, frequency, and duration of behaviors; and impressionistic ratings of behavior–situation units (Uher and Asendorpf 2008). Although methodological differences can shroud comparisons among species, Gosling and John (1999) found broad support for the basic personality dimensions related to sociality, anxiety, and cooperativeness in a number of other animals, from octopuses to chimpanzees. Although species-specific dimensions outside of those that differentiate humans exist (Uher 2008; Uher and Asendorpf 2008) and personality should encompass not only people but also behaviors and situations (Funder 2009), descriptions of stable, between-human personality differences as rendered in factor models usefully orient explorations of nonhuman primate personality structure. Differentiating individuals along basic personality dimensions provides a platform of traits for initial quantitative genetic

analyses of personality in primates. They are also good candidates for fitness correlates in evolutionary studies because these broad personality dimensions consistently relate to differences in health, longevity, and other social outcomes in humans (Roberts et al. 2007).

Studying multiple species with the same instrument also aids phylogenetic comparisons of personality structure by revealing the historical patterning of the emergence and modification of personality dimensions (Weiss and Adams 2008). This chapter next reviews factor model perspectives before considering how personality traits can evolve. However, behavioral and functional approaches make their appearance later when we need to causally connect broad personality variation to fitness (see Sect. 6.5.3). Assessments of behavioral profiles (Shoda and Mischel 2000; Uher et al. 2008), in particular, show promise for reaction-norm studies of personality evolution (see Sect. 6.6).

6.2.1 *Models*

One of many models for human personality describes personality differences in five independent dimensions (Digman 1990): generally speaking, differences in sociability and assertiveness are called Extraversion; variation in trust and cooperation are grouped as Agreeableness; Conscientious describes differences in discipline, planning, and self-control; variation in curiosity and creativity is captured by Openness; and a dimension called Neuroticism differentiates individuals in terms of anxiety, emotional stability, and stress response. Reasonably, it is referred to as the Five-Factor Model (FFM). A single individual is characterized by a stable density distribution along each of these dimensions (Fleeson 2001). The FFM is robust across cultures (McCrae et al. 2005) and emerges whether people are measured on items that are adjectival descriptors (Digman 1990) or cognitive-affective reactions to situations (Denissen and Penke 2008). This factor-model description of human personality has served as the starting point of several investigations of nonhuman primate personality.

Chimpanzees share with humans the broad dimensions of the FFM, with the addition of Dominance, which describes differences in competitive facility (King and Figueredo 1997). As a personality trait in primates, Dominance should be distinguished from social dominance or rank as the latter is an outcome rather than an aspect of personality (Hinde 1978; Buss 1988; Gosling and John 1999). The chimpanzee dimensions Agreeableness and Openness were given names identical to their human homologues. Although the labels differ, the remaining three traits map human equivalents: Surgency onto Extraversion, Emotionality onto Neuroticism, and Dependability onto Conscientiousness. Although chimpanzee Conscientiousness is more narrowly defined than its counterpart in humans (it does not include facets related to trustworthiness and duty) the Conscientiousness personality dimension seems to be a derived character in humans and chimpanzees, as it has not appeared

as a “pure” construct in any other species investigated (Gosling and John 1999; Weiss et al. 2006; Weiss et al. *in press*). Chimpanzees can also be differentiated from each other by their behavioral signatures, including propensities to set upon or affiliate with conspecifics, anxiety and arousal in stressful situations, curiosity toward novel foods and objects, impulsivity, goal pursuit, and physical and sexual activity (Pederson et al. 2005; Uher et al. 2008; Uher and Asendorpf 2008).

Gorillas likewise can be differentiated by their behavioral repertoires, similar to chimpanzees (Uher et al. 2008). Gorillas have also been described under the rubric of the human FFM using the dimensions Extroversion, Understanding (i.e., Agreeableness), Fearfulness (i.e., Neuroticism), and Dominance (Gold and Maple 1994). Salient in their absence from gorilla personality are homologues of human and chimpanzee Openness and Conscientiousness. Do gorillas really not differ in levels of curiosity and self-control, or were researchers just not looking for variation in these traits (Gosling and John 1999; Weiss et al. 2006)?

The importance of being more thorough can be seen in Weiss et al.’s (2006) portrayal of orangutan personality using a similarly broad instrument previously applied to chimpanzees (King and Figueredo 1997). Orangutans can be described with the dimensions Dominance, Extraversion, Agreeableness, Neuroticism, and Intellect. Intellect appears to be a blend of Openness and Conscientiousness.

A variety of models using impressionistic ratings have emerged to describe rhesus macaque personality. Some early studies revealed, alternatively, three dimensions: Fear, Hostility, Affiliation (Chamove et al. 1972) or Excitability, Sociability, Confidence (Stevenson-Hinde and Zunz 1978; Stevenson-Hinde et al. 1980). Later studies derived four dimensions: Tense–Fearful, Aggressive, Solitary, Curious–Playful (Bolig et al. 1992) or Sociability, Confidence, Excitability, Equability (Capitanio 1999). Rhesus macaques can even be described in as many as six dimensions: Confidence, Friendliness, Dominance, Anxiety, Openness, Activity (Weiss et al. *in press*). These results demonstrate the vagaries of measuring personality with instruments that have been incompletely adapted from studies of other species (Uher and Asendorpf 2008). That said, despite the various labels and differing numbers of components, many of these dimensions describe the same constructs. The primate dimensions of Extraversion are captured by Affiliation/Sociability/Solitary, Agreeableness by Hostility/Aggressive/Friendliness; Neuroticism by Fear/Excitability/Tense–Fearful/Confidence–Anxiety; Openness by Curious–Playful/Openness; and Dominance by Confidence/Dominance (Gosling and John 1999; Weiss et al. *in press*). This lumbering development matches the slow growth and refinement in characterizing broad dimensions of human personality chronicled by Digman (1990). We will not get there all in one go.

Using behavioral codings, Rouff et al. (2005) identified three dimensions of overall behavioral variation and four of between-individual differences in the personalities of lion-tailed macaques. The components that differentiated individuals (in contrast to behavioral occasions irrespective of the individual exhibiting them) map roughly onto the rhesus macaque dimensions Friendliness, Dominance, Activity/Confidence, and Anxiety. Although methodological and sample-size differences between these studies make for a knotty comparison, they suggest that several broad

features are conserved in the genus *Macaca*. It also shows that basic dimensions can shine through even if the instrument or ethogram is not specifically designed to find them. For instance, Rouff et al. (2005) chose behaviors that defined Neuroticism-like bipolar facets, namely, Anxious–Relaxed and Reactive–Unreactive. Each pole of these facets, however, did not group together. Reactive clustered with the Confidence-like component, and Relaxed and Unreactive loaded on the Anxiety-like component. This tallies with the claim that primate Neuroticism can become uncoupled into two independent dimensions describing free-floating versus situationally determined anxiety (Weiss et al. *in press*). Further work on lion-tailed, rhesus, and other macaque species is needed to clarify personality structure within this genus.

Whole personality structures have been educed in other Old World monkeys. Vervet monkey personality consists of three dimensions – Social Competence, Playful, Curious, Opportunistic Self-Serving (McGuire et al. 1994) – which map to the great ape domains of Dominance, Openness, and Agreeableness, respectively (Gosling and John 1999).

Konečná et al. (2008) extended the search for nonhuman primate personality structure to colobines. They investigated male Hanuman langur personality using both impressionistic descriptors and behavioral codings. Male langur behavior exhibits a three-dimensional structure consisting of Dominance, Involvement, and Activity. Impressionistic ratings also revealed three dimensions, called Agreeableness, Confidence, and Extraversion. High Agreeableness was expressed behaviorally by low Dominance; high Confidence by high Dominance and Involvement and by low Activity; and high Extraversion by elevated Activity. Again, these dimensions broadly match those found in other primate species, and the absence of other distinct dimensions (such as Openness) have reasonable ecological explanations (e.g., langurs are opportunistic foragers).

Over the years other, more specific aspects of personality and temperament have been examined in nonhuman primates (Clarke and Boinski 1995). Factor models and behavioral profiles by no means cover all the facets of primate personality that have been discovered. Attempts to describe all the features of between-individual personality differences, however, are starting to pay dividends by distinguishing the separate threads that we need to weave the historical patterns of primate personality evolution.

6.2.2 Building Blocks

Gosling and John (1999) showed that dimensions analogous (and perhaps homologous) to the five human factors appear in other species, with the addition of two dimensions, Dominance and Activity. Although Dominance is a salient dimension across many species, they found little evidence for Activity as a separate dimension. Nonetheless, activity is a common trait explored in behavioral–ecological investigations of personality (Réale et al. 2007) and was found to define a separate dimension in

wild langurs (Konečná et al. 2008) and rhesus macaques (Weiss et al. *in press*). Furthermore, in humans, although this dimension is subsumed under Extraversion in adults, it can emerge as a separate feature in adolescent males (John et al. 1994).

As it is possible for traits that normally vary together to become uncoupled during development (Groothuis and Carere 2005), we can consider the developmental evolution and phenotypic integration of personality dimensions. Correlated variation in the rudimentary personality structures of humans, chimpanzees, orangutans, and rhesus macaques can be described with a set of eight “basic” and five “blended” personality traits (Weiss et al. *in press*). The basic traits are called Sociability, Activity, Altruism, Anxiety, Confidence, Dominance, Openness, and Conscientiousness. The other traits are combinations of these components. In humans, chimpanzees, and orangutans, Sociability and Activity positively covary to form Extraversion; and Anxiety and Confidence negatively covary as Neuroticism. In rhesus macaques, in contrast, Sociability fluctuates with Altruism and is denoted as Friendliness. Meanwhile, in humans, Altruism and Dominance negatively covary in the dimension that describes cooperative behavior (i.e., Agreeableness), whereas orangutans have an interesting blend of Openness and Conscientiousness called Intellect. Positing these different basic traits follows the suggestion of Réale et al. (2007) to start defining possible categories of correlated suites of behavior beyond those already considered in work on behavioral syndromes (i.e., shyness–boldness, exploration–avoidance, activity, aggressiveness, sociability). These basic traits may be the result of opportunities for adaptive behavioral variation for meeting the social, ecological, and developmental challenges faced by big-brained, gregarious, long-lived mammals. Factor models for each species are the first step in hypothesizing the building blocks constituting primate personality structures.

Why we should find this historical patterning in primates or even whether we have the right “basic” dimensions are big questions. When thinking about the evolution of personality dimensions, it might seem strange at first to consider the evolution of something that is only a construct describing differences between individuals. Extraversion, for instance, describes differences between individuals in their sociality and action. Unlike a new behavior or organ, a personality dimension is not an obvious thing that a single individual has. However, this thinking takes a rather narrow view of what evolution is or how it effects populations. Selection does not act only on the mean level of a trait. Evolutionary change can occur on higher moments (e.g., variance, skew, kurtosis) of the population distribution of a trait as well as its covariance with other traits (Rice 2004). The genetic and environmental factors contributing to personality can start and stop covarying as the population evolves.

Before worrying too much over these complications, let us start more simply. When a population experiences selection, how does it respond? Let us go into the wild and find a troop of apes that differ in Extraversion. We measure their personalities and find, as it happens, that only individuals who are a value of S below the population mean in Extraversion are having children. For the moment, do not worry about why this might be the case. How sociable should we expect these offspring to be? Here, S is the selection differential (the amount that the parents producing

offspring deviate from the average trait value), and we want to know by how much the offspring will also differ from the parental average (or the response to selection, R). We are asking $R = ? \times S$ and the answer should have something to do about the resemblance between parents and their offspring.

6.3 Heritability

Heritability captures the resemblance between relatives. Heritability (h^2) is the proportion of the difference in phenotypes attributable to differences in inherited genes and thus ranges from 0 to 1.0. When considering two traits, we can also ask to what extent they are influenced by the same set of genes and what the direction of this relationship is. This is the genetic correlation (r_A) and can extend from -1.0 to $+1.0$. Behavioral traits are generally less heritable than morphological traits (Stirling et al. 2002). The heritability of personality and related traits has been established in several species of nonhuman primates. However, it is important to keep in mind that genes are not the only factor of interest in explaining variation: for certain problems, other types of environmental variance may be equally compelling to the researcher. As we shall see, although all sources of variation should be examined, differences caused by the additive effects of genes (called heritability) hold special status in the origin of both adaptive and neutral variation among individuals. The first step is to consider the extent of heritability in nonhuman primate personality.

Weiss et al. (2000) estimated the heritability of the six factors of chimpanzee personality. Of these factors, only Dominance was found to be significantly heritable ($h^2 = 0.63$). The estimate for Dependability was 0.21; although not detectably greater than 0, this suggests low to moderate heritability. The remaining traits showed little or no heritability. Importantly, this study of zoo-housed chimpanzees also established that very little of the differences in personality could be accounted for by differences among zoos. A later study using a different estimation technique (see Sect. 6.3.1) confirmed the high heritability of Dominance ($h^2 = 0.66$) and established the high genetic correlation with subjective well-being ($r_A = 1.00$) (Weiss et al. 2002).

The heritability of facets of personality and other related traits has also been investigated in nonhuman primates. Williamson et al. (2003) estimated the heritability of fearfulness and anxiety in rhesus macaques. Several aspects of their responses, such as a tendency to explore novel environments (latency to leave the protection of their mother during a Free Play Test) or to approach novel objects (in this case, a kiwi fruit) had estimated heritabilities of 1.0. These high estimates of heritability in these types of trait were confirmed in a later study with a similar measure of vigilance ($h^2 = 0.98$) (Rogers et al. 2008). Latency to approach strangers (measured as a Social Impulsivity Index) is also heritable in vervets, but only moderately so ($h^2 = 0.34 \pm 0.11$) (Fairbanks et al. 2004). There was no effect from the maternal environment, which given how it was estimated includes nonadditive genetic variance

from dominance and epistatic effects as well as the influence of maternal care and the mother's genotype. The Social Impulsivity Index consisted of two subscales measuring approach–avoidance and aggressiveness that were themselves highly genetically correlated ($r_A = 0.78 \pm 0.12$), suggesting that the two facets are influenced by a similar set of genes.

These results are not surprising given that the heritability of personality dimensions in humans has been estimated to be in the range of 0.4–0.8 (Riemann et al. 1997; Bouchard and Loehlin 2001), depending on the population and whether personality is assessed with self-reports, peer-reports, or both and are of similar magnitude in other animal species (van Oers et al. 2005a). The lack of a maternal effect in vervet impulsivity is also consistent with the small influence of shared environment (e.g., maternal care experienced by siblings) on personality in humans (Bouchard 1994; Rowe 1994).

6.3.1 *Estimating Heritability*

It is worth taking a step back and considering what heritability is and how it can be estimated. The basic question is how do parents and offspring resemble each other; that is, what is the covariance between mean offspring and mean parental phenotypes? Second, what proportion of variation among the offspring is caused by variation inherited from their parents? This value is found in the coefficient from a linear regression of offspring on parental phenotypes (Falconer and Mackay 1996), or

$$\beta_{z_o, z_p} = \frac{\text{cov}(z_o, z_p)}{\text{var}(z_p)},$$

where $\text{cov}(z_o, z_p)$ is the covariance between the phenotypes of offspring and their parents, and $\text{var}(z_p)$ is the phenotypic variation of the parents. This quantity describes how traits are selected (see Sect. 6.3.2) (Rice 2004).

Like the derivation of many basic statistical terms (e.g., “split-plot”) from agricultural experimentation, the meaning of many of the concepts surrounding the estimation of heritability are clearer once their origins in animal and plant breeding are understood. If you are raising livestock and are picking individuals to mate with one another to produce a new generation, what information do you want about these parents? What interests you is not the phenotype of each parent but, rather, the average phenotype of a parent's offspring. An individual's “breeding value” is a score representing their offspring's expected phenotype when mating is random (Falconer and Mackay 1996). Breeding values act additively – which is to say that an offspring's expected breeding value is the average of its parents' – and are thus thought of as caused by genes (not genotypes) that are passed from parents to their offspring. The effects of these genes act additively because they influence the phenotype independent of the constitution of the rest of the genotype, which is not the case for dominance or epistatic interactions.

The part of differences in phenotypes that can be attributed to breeding values is called the additive genetic variance of a trait. The ratio between additive genetic (V_A) and phenotypic variance (V_p) is an estimate of heritability

$$h^2 = \frac{V_A}{V_p}$$

because, assuming certain conditions apply, these genes are what determine the parent–offspring resemblance (Rice 2002). These assumptions are the following: (1) an individual’s phenotype is a combination of the additive genetic effects from both its parents plus an effect from the environment (there is no influence from dominance or epistasis); (2) mating is random; (3) genotypes are independent of the environment in which they are expressed; and (4) parents do not transmit their environment to their offspring. To the extent that these conditions hold, V_A/V_p can be used to estimate β_{z_o, z_p} , and in practice this is what is done.

Heritability can be estimated in a number of other ways, depending on the relationship between the individuals measured, such as twins (Martin and Eaves 1977) or half-siblings (Falconer and Mackay 1996). Entire pedigrees – describing not just the relatedness between parents and offspring or among siblings but between all relatives – can even be combined into a single analysis using the squared differences of phenotypes between all individuals (Grimes and Harvey 1980), which was shown to be an improvement over analysis of variance-based estimation techniques (Bruckner and Slanger 1986a, b). Like other, more advanced methods, this requires determining the relatedness of all individuals in the study population from a pedigree.

More recently, animal breeders and evolutionary quantitative geneticists have begun to favor variance component analysis, also known as random effects or mixed effects models, for estimating genetic and environmental sources of individual differences (Henderson 1950, 1975; Shaw 1987; Lynch and Walsh 1998; Kruuk 2004). These models still use all relationships in the pedigree; but, rather than pairing or nesting individuals together as in the techniques described above, breeding values are determined for each individual. Because the analysis occurs at the level of individual animals, this model was dubbed the “animal model” (Lynch and Walsh 1998). This set of equations can also be described as a mixed-effects model because it differentiates fixed effects (which account for mean differences among groups of individuals) from random effects (which partition the remaining variance between individuals). Breeding values are the typical random effect of interest. Although the meaning of “fixed” versus “random” effects are quite varied (and confused) in the literature (Gelman 2005), it is by these terms that evolutionary geneticists are trying to distinguish known causes of differences between classes of individuals (e.g., sex and age) from those that govern a trait’s variance and for which each individual has its own value. An advantage of the animal model is that it can incorporate, and therefore estimate, other sources of variance. (See Chap. 7 for effects of interest in animal personality research.) Animal models have been used successfully on data from wild populations to estimate components of

variance in addition to heritability (Kruuk 2004; Kruuk and Hadfield 2007) and are particularly suitable when trying to distinguish genetic from environment effects (Kruuk and Hadfield 2007). Variance components and breeding values for the animal model can be estimated with restricted maximum likelihood (REML) methods (Shaw 1987; Lynch and Walsh 1998) or using Bayesian analysis (Sorensen and Gianola 2007; O'Hara et al. 2008; Hadfield et al. 2010).

In quantitative genetics of natural populations, these effects can only be identified if they differ between individuals so variance component decomposition does not provide a complete causal account of how a trait comes to be (component terms such as V_A or V_E are also referred to as causal components of variance) (Falconer and Mackay 1996). Take a look at maternal effects such as those from early rearing experience: work by Harlow (1969) showed the importance of a mother's love for the behavior and adjustment of an individual later in life. The mother clearly has an "effect." Although such differences can be induced in experimental conditions, there still might not be any maternal effects in the wild. Just because close maternal contact is developmentally necessary for proper fear and anxiety reactivity does necessarily mean that differences in rearing style influence offspring phenotypes. This lack of difference is what is meant if no maternal effect is found on a trait.

Estimates of heritability in nonhuman primates have drawn on all of these techniques, but it pays to use the method most suited to the available pedigree data. For estimating heritability in primate populations, the animal model is to be preferred. This is primarily because it can handle the arbitrary but interconnected pedigree structure of primates in different zoos (Weiss et al. 2000) as well as tolerate unknown relatedness such as missing paternity information common in studies of wild primates (de Ruiter and Geffen 1998). Furthermore, using all relationships from a pedigree improves estimates of genetic correlations (Åkesson et al. 2008). The ability of Bayesian methods to handle small sample sizes (O'Hara et al. 2008) and confounding variables (Ovaskainen et al. 2008) makes it suitable for analyses involving the hundreds of subjects available for primate research rather than the thousands typical in agricultural settings, for which REML procedures have been developed and refined. Bayesian methods are also good for evolutionary questions because the uncertainty in the prediction of breeding values can more easily be carried on to estimates of evolutionary change (Hadfield et al. 2010).

Whichever technique is used, it is important to realize that these are simply models of the transmission of traits from parents to offspring (Rice 2004). Estimating heritability is a process of fitting statistical parameters to data, and these estimates are influenced by more than just the variation in additive genes (Stirling et al. 2002). Many of the modeling assumptions (random mating, no gene-environment correlations) required to estimate heritability from a parent-offspring regression are unlikely to hold in primates. Furthermore, variance from the environment in these models is actually just the residual variance, or the error. This error includes all the causes of differences between individuals for which we do not know how to account. Even when we are assigning a name to a key component of variance, such as V_A , the most general descriptions of the parent-offspring resemblance do not

make any assumptions about what is being inherited. It is usually assumed that the transmission of DNA sequence variants accounts for this resemblance, but epigenetic sequences can be transmitted across generations and contribute to additive genetic variance in the same way (Johannes et al. 2008, 2009). Primate parents and offspring can resemble each other for nongenetic reasons as well, such as abusive rearing styles in rhesus macaques (Maestripieri 2005). That environments can be transmitted is a distinct possibility that is not without utility for evolutionary model building (Odling-Smee et al. 2003). As in the remake of a 1970s horror film, these snags in understanding heritability (Feldman and Lewontin 1975; Visscher et al. 2008) are the “undead” of quantitative genetics, particularly in the psychological sciences (Taylor 2010).

It is thus important in any discussion of heritability to have a handle on how it is being estimated and whether the model or design being used is appropriate to the data (Kruuk and Hadfield 2007; Hadfield et al. 2010). Similarly, animal models can be sensitive to the inclusion of fixed effects (Wilson 2008). Additive genetic variance estimates can change when adding a fixed effect that is genetically correlated with the trait.

When interpreting heritability as a statistic, there is little practical use in P values associated with testing the hypothesis that $h^2 > 0$. First, almost all psychological traits are heritable (Turkheimer and Gottesman 1991), so finding significant additive genetic variance should not come as a shock. Second, the sample sizes available for most primate populations often do not give enough power to distinguish heritability from zero, even if heritability is actually moderate. Finally, evolutionary geneticists are not interested in the predictive utility of heritability as it is practiced in animal and plant breeding, where a particular point estimate for h^2 is sought. What we are, instead, interested in is the range of likely values for h^2 that are supported by the data and by the model (typically the 95% coverage or confidence interval) to indicate whether heritability is low, moderate, or high.

6.3.2 *Why Care About h^2 ?*

In the age of molecular genetics, heritability may seem like an old fashioned or even outdated concept (Visscher et al. 2008). It may also appear quirky to put so much focus on genes (without naming specific ones) rather than on genotypes. Would we not like to know the specific genes that interact with each other and with the environment to determine an individual's personality? On a practical level, even if an investigation revolves around nongenetic variables, carrying out an analysis within an animal model framework allows estimates of the effects of these variables to be conditioned on familial resemblance. For answering evolutionary questions, heritability gets at those differences in genes that are required for the change of phenotypes through both random drift and natural selection and are therefore fundamental to the debate over how phenotypic differences are maintained in populations.

Going back to our hypothetical troop of more-or-less extraverted primates, heritability captures how much offspring are expected to resemble their parents. A linear regression, such as that of offspring on mid-parent phenotype, is also a model for predicting an offspring's phenotype from those of its parents. It can be used to predict the average personality level of the next generation from the mean level of the selected parents. Heritability thus answers our question of how the offspring of the less Extraverted parents will differ from their parents' generation. The potential for the mean phenotypic value of a trait to respond to selection is proportional to the magnitude of selection on the trait times its heritability. The equation expressing this relationship is called the breeder's equation,

$$R = h^2 S,$$

stating that a population's response (R) to selection (S) is limited by the heritability of the trait being selected. This equation can be expanded to more than one trait, in which case the response to selection of one trait is a function of its genetic variance and its covariance with other traits being selected (Lande 1979; Turelli 1988; Falconer and Mackay 1996), given by

$$\Delta z = \mathbf{G}\beta,$$

the multivariate breeder's equation, where $\mathbf{G}$ is a matrix of additive genetic variances and covariances of the traits, β is a vector of selection gradients on each trait, and Δz is a vector of responses to selection for each trait (see Blows 2007 for a review). When studying the evolution of personality, then, it is important to estimate not just the heritability of each dimension but also the genetic correlations among the dimensions and between personality and other traits (see Chap. 7). Thus, genetic correlations between behaviors is one way in which personality traits can be defined (Dingemanse and Réale 2005).

The centrality of heritability to the problem of quantitative variation comes from a basic mathematical result: both random drift and selection reduce additive genetic variance (Falconer and Mackay 1996). Much work on the evolution of personality has gone into developing theories about how individual differences in personality are maintained.

6.4 Persistence of Variation in Psychological Traits

The maintenance of heritable variation in traits is a long-standing problem in biology (Barton and Turelli 1989; Barton and Keightley 2002). Processes that maintain additive genetic variation in a trait may come through direct action on the trait or through indirect action on a genetically correlated trait (Robertson 1967).

In discussions of the "amount" of additive genetic variation, it is often pointed out that, as a ratio, the magnitude of heritability is as much a function of all other sources of variance (nonadditive genetic and environmental) as it is of V_A . To make

heritability comparable between traits and species, Houle (1992) defined the coefficient of additive genetic variation as

$$CV_A = 100 \frac{\sqrt{V_A}}{\bar{X}},$$

which standardizes V_A by the phenotypic mean, $\bar{X}$. However, calculating CV_A requires that the phenotype is measured on a ratio scale, meaning that it has a true zero value. Personality constructs in primates are typically formed on ordinal or interval scales, however. This coefficient, therefore, has little utility for comparisons among the heritability of many psychological traits. Furthermore, it loses the key interpretation of heritability as the covariation of parent and offspring phenotype, which is so key to the evolvability of a trait.

6.4.1 Processes Maintaining Variation

All genetic differences ultimately arise through mutation, so it is possible for genetic variance to be maintained by a balance between its introduction by mutation and its removal by selection (Lande 1979) or random drift (Barton and Turelli 1989). In biology, most of the debate involves theoretical considerations about the distribution of mutation effect sizes, the number of loci influencing the trait, and the extent of pleiotropy (Johnson and Barton 2005; see Penke et al. 2007 for a review of alternative models from the perspective of human personality evolutionary genetics). The problem with applying these models to the maintenance of genetic variation in nonhuman primate personality traits is that the data required to evaluate them are not available so the arguments are restricted to theoretical considerations. Until such a time as data are available, evolutionary studies of personality will focus on phenotypic and quantitative genetic data.

Even without comprehensive molecular genetic data, fitness trade-offs are essential to consider in the evolution of any trait (Lande 1982; Charnov 1989; Roff and Fairbairn 2007). Such incompatibilities arise when a change in one trait that increases fitness is accompanied by a change in a second trait that decreases fitness. Trade-offs are a particular focus of life-history theory where, for example, there might be alternative choices between fecundity and survival (Williams 1966b; Partridge and Sibly 1991). Because selection will have eroded variation that influences both traits positively, components of fitness tend to have negative genetic correlations even if the phenotypes are positively correlated (Lande 1982). The evolutionary effect that such trade-offs have is typically explored through genetic covariations (Roff and Fairbairn 2007). This brings us back to the multivariate breeder's equation (see Sect. 6.3.2): the potential response of a trait to selection is constrained by selection on other, correlated characters, expressed in the **G** matrix.

The interpretation of **G** as an expression of trade-offs between traits is not without controversy (Pigliucci 2006) because functional trade-offs between two traits (e.g., in resource allocation) can sometimes have a positive genetic correlation

(Houle 1991). In personality research, some of these broader problems can be avoided because we are not interested in predicting long-term responses to selection, which is the crux of much of Pigliucci's (2006) critique of evolutionary quantitative genetics. Trade-offs that can be posited by considering genetic covariances can also be seen when selection of correlated characters produces scenarios where different combinations of traits have equal fitness, potentially maintaining genetic variation in each trait (Roff and Fairbairn 2007). Beyond this, traits can be entangled developmentally through higher orders of epistasis in addition to genetic correlation (Rice 2004).

6.4.2 *Evolving and Resolving Explanations*

Evolutionary psychologists have given many explanations for the persistence of variation in human personality. These explanations have been grouped into three categories: adaptive, nonadaptive, and maladaptive differences (Buss and Greiling 1999). In evolutionary genetic terms, the categories can be rephrased. When speaking of adaptive or maladaptive differences, one is interested in traits that are causally related to fitness, without regard for "where" the variation is coming from (genes or the environment). Nonadaptive sources of difference include neutral variation that, although it may correlate with fitness, does not cause fitness differences; and "by-products of adaptive variation" (Buss and Greiling 1999) that come about through the correlated selection of some other trait. Given the recent shared ancestry and common personality structures between humans and nonhuman primates, explanations offered by evolutionary psychologists are a reasonable starting point for addressing variation in nonhuman primate personality.

Tooby and Cosmides (1990a) were the first to place personality squarely within a modern evolutionary framework, arguing that individual variation was the result of neutral evolution. Most of the variation in the traits that psychologists consider as personality would evolve by drift if behavioral tendencies that are stable across situations are not adaptive; this is because such general tendencies would not be solving any particular problem and thus be causally unconnected with fitness, that is, evolving neutrally. Although the effective population size in humans is large enough that drift is inadequate at reducing genetic variance in neutral traits, all the evidence connecting personality to differences in health, longevity, and reproductive success contradicts the required complete selective neutrality (Penke et al. 2007). MacDonald (1995, 1998) and Nettle (2006) argued instead that variation is maintained by balancing selection for personality differences as alternative behavioral strategies. Human personality dimensions can be cast as trade-offs (Nettle 2006) between mating success and exploration versus risk (Extraversion); vigilance versus the health consequences of stress (Neuroticism), mate attraction versus psychosis (Openness); short-term versus long-term fitness benefits (Conscientiousness); and altruism versus selfishness (Agreeableness). If this is the case, similar trade-offs are likely to manifest in nonhuman primates. As several of these mechanisms are being

investigated in primates (e.g., stress and cooperative behavior), an appreciation of individual differences would reveal whether these fitness trade-offs exist. For example, most primate interaction networks support the emergence of cooperation (Voelkl and Kasper 2009), so primate societies might contain a mix of cooperators and defectors who differ in Agreeableness. Other trade-offs that have not been put forward for humans have been observed in primates, such as decreased vigilance over infants displayed by rhesus macaque mothers while engaged in allogrooming (Maestripieri 1993).

A basic life-history trade-off has also been theorized to underlie human personality and intelligence differences (Rushton 1985; Figueredo et al. 2005; Rushton et al. 2008). This within-species difference in a developmental strategy of investing in fecundity or survival was theorized to extend in humans to family size, interbirth interval, and parental care (Rushton 1985). An individual would either pursue a risky life of multiple mates, large families, and little parental investment or a slow-paced existence with one mate, few children, and long life. Humans disposed toward the latter strategy were found to be less neurotic, more extraverted, more agreeable, and more conscientious (Figueredo et al. 2005). Rushton et al. (2008) combined this with the postulation of a general factor of personality (GFP) underlying the five human dimensions (Muek 2007) to suggest this single factor (capturing differences in cooperativeness and prosociality) is under directional selection along with the associated life-history traits (contra Figueredo et al. 2005, who proposed balancing selection). Although selection has not been estimated for the GFP, genetic analysis of twins showed that all of the genetic variance was attributable to dominance effects (Rushton et al. 2008), which matches a theoretical prediction of long-term directional selection (Falconer and Mackay 1996) and the finding that life-history traits have higher dominance variance (Crnokrak and Roff 1995).

The existence of a general personality factor in humans is a bit tender in its psychometric joints (Ashton et al. 2009), but this does not invalidate the study of life-history traits and personality in nonhuman primates. Personality traits may be separately linked to different life-history variables. In comparison with most other mammals of the same size, primates take longer to gestate and mature, have fewer offspring, and live longer lives (Strier 2003). There is also a significant amount of variation in life-history variables among primate species concerning the speed of gestation, development, and maturation adjusting to fit differences in body size, which is an adaptation to local ecology (Harvey and Clutton-Brock 1985). Trade-offs, then, exist at the within-species level. This can be seen in rhesus macaques, which exhibit a positive genetic correlation between age at primiparity and longevity, so females who start reproducing earlier have a shorter lifespan (Blomquist 2009b), suggesting that a fitness trade-off in life-history strategies potentially exists in non-human primates.

The life-history perspective on personality is also favored in theoretical work by behavioral ecologists (Dall et al. 2004; Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008). Personality differences are again conceived of as distinct behavioral strategies (Dall et al. 2004). This body of theory allows us to imagine under what conditions we would not have personalities at all. Two basic “personalities” can

coexist as stable types of competing strategies under frequency-dependent selection (Maynard Smith 1982). However, the same stable situation can emerge if each individual plays a mixture of both strategies. In this case, no personalities exist because each individual is expressing exactly the same behavioral tendency. Individual differences in behavior that can be dubbed personality can emerge, however, if these differences are tied to life-history trade-offs (Wolf et al. 2007; Biro and Stamps 2008). More generally, the fitness of a particular trait may depend on the frequency of other traits being expressed in the population rather than on the frequency of alleles affecting the target trait (Reeve and Dugatkin 1998). For example, the fitness implications of exploratory behavior might depend on conspecifics' aggression rather than on one's own level of exploration–avoidance. The output of such theory has so far been applied exclusively to studies of nonprimate animal personality from the framework of behavioral syndromes (Sih et al. 2004).

For rhetorical reasons, explanations of the persistence of variation in personality are often set up as mutually exclusive possibilities. This need not be the case and is probably an artifact of how selection is usually presented and contrasted (Rice 2004). Directional and stabilizing selection can co-occur on the same trait, changing different moments of the phenotypic distribution. Such possibilities should be exploited when considering how personality evolves (see Sect. 6.6).

Which approach is applicable for nonhuman primates? Both their close affinity with humans and the rich literature on their behavioral ecology (Strier 2003) suggest that combining methodologies from evolutionary psychology and behavioral ecology perspectives are feasible. From an evolutionary genetic perspective, the apparent commonality of several aspects of primate personality structure, such as dimensions related to sociality and anxiety, suggest that certain evolutionary equilibria are maintained over long periods of time in primates. If true, evolutionary genetic processes can be fruitfully investigated using phenotypic data (see Chap. 7). Resolving alternative explanations for the persistence of variation in nonhuman primate personality is particularly exciting because we can compare species that are closely allied because of phylogenetic affinity (e.g., macaques) or socioecological similarity (e.g., chimpanzees and spider monkeys). Nonhuman primates also offer a window through which to chase the evolutionary genetics of personality into the wild.

6.5 Evolution in the Wild

Studying the evolution of personality in primates means eventually studying personality in wild primates. Investigating the selection of personality can proceed along two courses: by relating personality to fitness differences or by indirect inference in comparing how correlations among personality traits differ between populations in varying environments (Dingemanse and Réale 2005). Evolutionary genetic studies in the wild have progressed tremendously through the use of extensive pedigree information, long-term data collection, and the identification of individuals (Kruuk and Hill 2008). Recognizing individual animals in the wild has been central

to traditions in primatology for at least 60 years (Matsuzawa and McGrew 2008). This acknowledgment of individuality and family life eventually led some primatologists to start tracking familial lineages (Kawai 1958; Kawamura 1958; DeVore 1962; Yamada 1963; Carpenter 1964; Goodall 1986). Given the many decades these pedigrees have been curated at some wild primate sites (e.g., Arashiyama, Cayo Santiago, Gombe, and Koshima), it is a wonder that this information has been used only sparingly for evolutionary and quantitative genetic research (the exceptions are, notably, captive populations, those at the Vervet Research Colony and the Southwest National Primate Research Center). More typically, pedigree information is used for the purpose of determining reproductive success, mate choice, and social relationships among kin (see Chap. 3). Quantitative genetic studies of wild primates offer rich, low-hanging fruit of which primatologists are now beginning to partake (Blomquist 2009a, b).

6.5.1 Pedigree Construction

In primates, maternity can be reliably inferred from behavioral data, as infants initially associate exclusively with their mothers (Strier 2003). Paternity is more tricky and typically requires exclusion or likelihood assignment using genetic markers. Currently, the most prevalent molecular markers for pedigree construction are microsatellites (Jones and Ardren 2003). The advantages of microsatellites are that they are relatively easy to discover in new species, are codominant (both alleles can always be recognized, if they differ), are highly variable (making it easier to distinguish individuals), and can be obtained from wild samples (Pemberton 2008). With these markers, a number of algorithms and statistical techniques can be used to assign paternity (Jones and Ardren 2003; Pemberton 2008). For evolutionary genetics, pedigree accuracy is a constant concern because errors lead to imprecision in heritability estimates (Kruuk 2004).

Building pedigrees also allows detection of inbreeding. In primates, inbreeding is primarily a concern in isolated, endangered, or captive populations (e.g., Alvarez et al. 2009). Although the role of inbreeding depression in personality has not been investigated directly (Penke et al. 2007), there is evidence suggesting that it is a possibility (Rebello and Boomsma 2007).

6.5.2 Fitness Is Not What You Think It Is; Rather, It Is Exactly What You Think It Is

“Fitness” is an inconsistently used term in evolutionary studies, with evolutionary psychology being no exception. Many workers have taken definitions of fitness that attempt to distinguish the effect of random drift from that of natural selection. Writing on the subject, authors often adopt, knowingly or unknowingly, Williams’s (1966a)

definition of fitness as the average reproductive success of a given “design.” For example, Grafen (1988) acknowledged Williams in distinguishing individual lifetime reproductive success from fitness, and Penke et al. (2007, p. 553) described fitness as a property of a genotype, with “its statistical propensity for successful reproduction.” Yet these distinctions are not necessary. The cleanest definition marks fitness as an individual’s contribution to the next generation, and it is thus a property of individuals and not of genotypes or of alleles (Rice 2004). This interpretation includes both selection and drift in an individual’s reproductive success, the difference being whether the covariance between genotype and fitness is random (drift) or nonrandom (selection). It is thus a question of causality.

Lifetime reproductive success is therefore the canonical measure of fitness, but individual differences leading to reproductive success can enter at any stage in an organism’s life – the where and when having considerable practical import. Four general components of fitness include survival to breeding age, reproductive lifespan, fecundity, and offspring survival (Brown 1988). Assuming parentage can be assigned, these data can be (and are being) tracked in wild primates. Whichever component of fitness is used, selection is measured with it in the same way. The first step is to test whether the trait of focus is significantly related to fitness (Mitchell-Olds and Shaw 1987) by regressing the trait on fitness. Because annual and lifetime breeding success are not normally distributed but, rather, follow a zero-inflated Poisson or negative binomial distribution, where each year in an animal’s life is a chance to “fail” at having an offspring, a generalized linear model should be used instead of an ordinary least-squares regression (Kruuk et al. 2002). The next step is to estimate the strength and mode of selection by regressing the standardized trait on relative fitness as the linear coefficient (for directional selection) or twice the quadratic coefficient (for stabilizing or disruptive selection) using an ordinary least-squares method (Arnold and Wade 1984; Stinchcombe et al. 2008). Because there are competing hypotheses about the role of selection in maintaining variation in personality, it is essential to avoid the publication bias that plagues estimates of the strength of selection (Kingsolver et al. 2001). Given the present state of knowledge on personality in the wild, the absence of selection is as interesting as its presence (Dingemanse and Réale 2005) because we would like to know under what ecological conditions personality differences are adaptive in primates and when they are only neutral.

Selection coefficients of personality traits are already being estimated in wild populations of nonprimate animals (Dingemanse and Réale 2005), so primatologists should follow the lead of behavioral ecologists in applying the tools of evolutionary biology to personality (in contrast to doing psychology with their evolutionary-paradigm beanie on). A difficulty in following this path is that in current studies of nonhuman primate personality, lifetime reproductive success is usually not available simply because the study subjects are still alive. Research on living individuals must then use other components of fitness, such as age at primiparity, interbirth interval, annual reproductive success, or infant survival. Investigations of personality in populations of wild primates are barely embryonic, but a future goal of this research should be longitudinal studies that ultimately measure the implications of personality differences for lifetime reproductive success.

6.5.3 *G Matrices Gone Wild*

The use of the additive genetic variance–covariance matrix runs into a spot of trouble when taken out of the farm and into the jungle. In agricultural and laboratory conditions, the predictive value of the breeder’s equation works because we decide which traits to select. In the wild, however, we can never be certain that we are including all the characteristics that are being selected (Lande and Arnold 1983; Endler 1986). This is one explanation for why, in wild populations, the phenotypic response to selection can be either zero or even opposite of what is predicted from the **G** matrix and the vector of selection gradients (Merilä et al. 2001).

Another general difficulty that must be resolved in the particular is the leap from the estimation of selection gradients to inferences about adaptation (Grafen 1988). Here, we are seeking functional and causative accounts for how personality and life-history variables lead to differences in reproductive success (Pigliucci 2006). In the troop of primates where we find only the introverts having children, is the negative correlation between Extraversion and breeding success chance sampling variation (i.e., genetic drift), or is this connection causal, meaning that there is selection for low Extraversion? In building causal models to distinguish direct selection from indirect selection or random drift, it is essential to have a more complete functional and behavioral understanding of personality differences. In nonhuman primates, personality dimensions based on adjectival descriptors do not enjoy a one-to-one mapping with independent aspects of behavior (Konečná et al. 2008). In langurs, both Confidence and Extraversion correlate with the behavioral dimension Activity, but Confidence is also related to the Dominance and Involvement behavioral components. It is likely that impressionistic dimensions capture personality traits that can be expressed through different aspects of the same behavior, such as the frequency and bout length of grooming sessions. This is precisely the point where behavioral repertoire and syndrome approaches will be of most use in the evolutionary genetics of nonhuman primate behavior, where a syndrome or profile can identify the situational and behavioral units that correlate. Such procedures promise to untangle the ecological variables defining the situations in which personality is differentially expressed and provide testable paths through which trait personality differences might be affecting life-history outcomes and reproductive success.

6.5.4 *Into the Wilds of Personality*

Although personality researchers can borrow techniques for estimating heritability and selection from evolutionary quantitative geneticists, they are still faced with the problem of collecting personality data on wild animals. Studies that specifically take ecological or evolutionary paths to discovering and defining personality traits are sorely lacking on nonhuman primates (Uher 2008). In addition to highlighting the need to investigate species-specific differences in personality constructs (Uher 2008; Uher et al. 2008), we also need to be open to the possibility of

the same species exhibiting alternative personality structures in different ecological environments (Bell 2005; Uher 2008). Another barrier to educing a whole personality structure of a species in the wild is the number of different populations that can be studied. The incorporation of Openness-like facets into the Extraversion dimension of Hanuman langurs (Konečná et al. 2008) could be peculiar to the population rather than to the species. The small sample of langurs ($n=27$) is not necessarily fatal, as a fully informative factor structure can be recovered from small samples if the number of factors is small and the number of items large (de Winter et al. 2009). Furthermore, as the chimpanzee factor model replicated in different populations (King et al. 2005; Weiss et al. 2007, 2009), there are unlikely to be broad structural differences between primate populations of the same species, as defined by factor models of personality. Understanding the ecologically relevant differences in primate personality expression, then, requires the finer lens of behavioral repertoire and allied approaches.

A standard adjective rating instrument, such as the Hominoid Personality Questionnaire,¹ can be used to obtain an initial impression of species whose personality has not been previously measured. First, this allows initial integration into other findings about personality structure and will help resolve unknown questions about the historical patterns of personality evolution. Second, as a practical matter, impressionistic ratings can be gathered from raters who, although familiar with the individual animals in the study population, may not have been studying their behavior. Finally, behavioral repertoires might differ between populations (because of slight differences in ecological situations) more than the personality structure is likely to differ.

6.6 Personality As a Norm of Reaction

An interaction between a genotype and a set of environments is called a reaction norm (Dobzhansky 1955; Platt and Sanislow 1998 and references therein). Plots showing hypothetical reaction norms of different genotypes in different environments litter psychology textbooks (Platt and Sanislow 1998) and come up repeatedly in contentious debates about nature and nurture (e.g., Sternberg and Grigorenko 1997). Accounting for these effects will take real work, not just chatter about *Arabidopsis*, *Drosophila*, and *Mus*. Models that estimate variance from $G \times E$ interactions have started making their way into psychological research (Johnson 2007). The concept of a behavioral syndrome explicitly incorporates the idea of personalities as norms of reaction (i.e., a correlated suite of responses across environments) (Sih et al. 2004) and captures the idea that personality depends on context (van Oers et al. 2005b). Envisioning personality in this way may allow behavioral ecologists

¹Available from Alexander Weiss.

to bypass much of debate between person–situation and ordinary trait perspectives on personality (Penke et al. 2007). However, a norm-of-reaction approach offers a much greater potential for integrating between- and within-individual variation in personality to the intrepid primate psychologist willing to grapple with a few more complexities in their models.

Looking at personality as a reaction norm may fuse various perspectives on personality when we incorporate tools from quantitative genetics (van Oers et al. 2005a). Mischel and Shoda's (1995) person $\times$ situation perspective on personality, which looks for stable behavioral profiles, can be recast in terms of reaction norms (Penke et al. 2007). Penke et al. (2007) also noted that Mischel and Shoda (1995) focused their theory on describing individual reaction norms but that as aspects of these behavioral profiles are heritable (Borkenau et al. 2006) it is more appropriate to examine the $G \times E$ level of reaction norm differences. However, the individual reaction norm should not be discarded, even if what we are interested in is genetics.

The $G \times E$ reaction norms are typically investigated using experimental designs that subject a set of genotypes to different environments to assess the phenotypic plasticity of each genotype (Via et al. 1993). What do we do with primates, however, who are generally not keen on being cloned or grown in experimental plots? To the extent that a personality trait varies within an individual, it is a labile trait, changing throughout the course of life (Gomulkiewicz and Kirkpatrick 1992; Lynch and Walsh 1998).

Because personality can be measured multiple times, either in different situations or as the individual ages, it can also be examined using individual reaction norms (Nussey et al. 2007). Individual reaction norms encompass all of the situations and environments in which an individual expresses a trait throughout life. Reaction norms can be scrutinized at both the individual phenotypic and genotypic levels. An individual reaction norm covers person $\times$ situation (or environment) variance at the phenotypic level, whereas the genetic reaction norm describes $G \times E$ interactions. Differences in reaction norms may exist at either level (or none or both). These reaction norms have a physiological basis, as seen in rhesus macaques, who have stable serotonin concentrations in early life as they experience a number of stressful events during emigration (Mehlman et al. 1995). The nongenetic variance in individual reaction norms is attributed to permanent environment effects, which for personality could include the influence of early development or of learning. Individual reaction norms can be studied with quantitative genetics using a random regression animal model (Gomulkiewicz and Kirkpatrick 1992; Nussey et al. 2007), which, using repeated measures of personality in different situations and pedigree data, can distinguish the permanent from the genetic sources of interaction variance.

The chief practical difficulties of this approach for the evolutionary genetics of primate personality are twofold. The first is the partition of environments. What situations are considered the same environment in which a personality trait is being expressed? Plus what is a situation? Second, the sample sizes needed to obtain good estimates of these parameters will be arduous to muster for nonhuman primates. Hopefully, primatologists are up to this challenge (van Oers et al. 2005a).

6.7 Conclusion

Reaction-norm representations of the expression, development, and evolution of behavior may be able to separate out the genes, situations, and vagaries of existence that go into determining an individual primate's personality. However, these approaches by themselves have little hope of putting an end to the nature–nurture debate because we cannot fathom that nature + nurture is a model.

The focus here has been on variance component models that break down the causes of personality and of measuring selection on the phenotypic level because this is what the data from most current studies of wild nonhuman primates can support. Researchers familiar with their primate subjects, even if they do not study behavior, are a resource for getting initial impressionistic ratings from which a personality structure can be defined. Once this structure is known and compared within its phylogenetic context, researchers can ask the salient behavioral and ecological questions of why we find a particular personality structure in each species. Many primates live together in groups where kin can be identified and tracked as individuals throughout their lives, supplying information about genetic relatedness and life history needed for evolutionary genetic studies of personality. Ethological investigations of more specific aspects of personality can be used to connect personality differences to fitness-relevant outcomes. To the extent that personality hinders or helps individual or group adaptation to habitat disruption, a thorough understanding of nonhuman primate personality may aid conservation efforts.

Taking evolutionary quantitative genetics more broadly, we should aim to investigate primate personality through population genetics, genomics, and molecular ecology. These techniques are already being used to study the evolution of primate phenotypes, such as coloration, for which specific gene variants have been identified (see Chap. 14). Comparing homologous and convergent personality traits among primate taxa would highlight ecological conditions that pattern structural divergence between species as well as guide the evolutionary study of psychological traits out of the morass of “environments of evolutionary adaptedness” (Symons 1979; Tooby and Cosmides 2005). This would further involve finding gene variants and quantitative loci underlying personality differences, detecting differences in gene frequencies among populations of the same species, and looking for molecular signatures of past selection and demographic changes that explain extant variation in primate personality.

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